Fish Community and Environmental Effects on Lake Trout

Lake Trout Synthesis
Community Biology Working Group
1990

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ABSTRACT

Carl, L., M.-F. Bernier, W. Christie, L. Deacon, P. Hulsman, D. Loftus, D. Maraldo, T. Marshall, AND P. Ryan. 1990. Fish community and environmental effects on lake trout. Lake Trout Synthesis, Ont. Min. Nat. Resour., Toronto. 47 p.

Angler effort explained over 70% of the variation in the sport angler harvest of lake trout (*Salvelinus namaycush*), indicating that angling data do not allow a valid test of fish community effects with angled lake trout as the dependent variable. Higher standing stocks of lake trout tend to occur in small lakes with few or no other fish species present, due to lower trophic level transfer costs. Lakes with coregonines as prey will provide larger lake trout, due to the bioenergetic advantage of large size prey to individuals over invertebrates as prey, but have lower standing crops because of increased trophic level transfer costs, compared to lakes with only invertebrate prey for lake trout. Annual lake trout population data collection on monitored systems is essential to separate out stochastic sources of variation from man-induced changes.

The prey species available was found to affect lake trout growth, while the presence of predators negatively affected the relative abundance of lake trout. These results indicate the fish community concept is relevant and should remain as the basis of the Fisheries Assessment Unit (FAU) program until it can be tested more rigourously. Measures of other members of aquatic communities may also be important to lake trout communities. These measures, such as the presence of *Mysis*, zooplankton size structure and fish size frequency distribution, should be examined further for relevance in explaining variation in lake trout population parameters.

Keywords: Fish community types, lake trout growth and yield, fish particle size, non-fish indices

INTRODUCTION

This paper examines aspects of the relationship of the aquatic community to lake trout (*Salvelinus namaycush*) biology and yield. We review the fish community type (FCT) concept, its relevance to managers and alternative schemes for grouping lakes for management purposes.

Symposia such as the Salmonid Communities in Oligotrophic Lakes (SCOL) (Loftus and Regier 1972) and the Percid International Symposium (PERCIS) (Colby 1977) reported that fish communities of similar species composition tended to respond in a similar manner to stresses and management actions. Following the results of SCOL and PERCIS, a lake classification system was developed in Ontario to define groups of lakes for the purpose of assessment and management (Ontario Ministry of Natural Resources (OMNR) 1978). It was anticipated that long-term monitoring and experimental management on a subset of each FCT would provide generalities which could be extrapolated to lakes of the same FCT across the province and lower the cost of managing lakes while increasing our knowledge base (OMNR 1978). This logic assumes that there are fundamental differences among lakes classified in such a manner (i.e. by FCT), and that lakes of a particular FCT respond to stress in a similar way. A series of Fisheries Assessment Units (FAUs) were established across Ontario to collect the requisite data (OMNR 1978). Fish community types (FCTs) were defined on the basis of the occurrence of six species of primary interest to lake managers. The fish species included in this classification system (and often referred to as "major" species) were brook trout (*S. fontinalis*), lake trout, lake whitefish (*Coregonus clupeaformis*), northern pike (*Esox lucius*), smallmouth bass (*Micropterus dolomieui*), and walleye (*Stizostedion vitreum vitreum*).

In this paper, we examine groups of lakes classified by FCT for significant differences in lake trout parameters. Initially, we explored the degree to which FCTs with lake trout were associated with specific abiotic lake characteristics, as this might mask possible community effects on lake trout yield. We then tested for differences in lake trout yield among FCTs. Unfortunately, small sample sizes restricted our ability to perform all appropriate statistical tests, or to examine the FCT in relation to other lake trout parameters. There are 32 FCT combinations with lake trout, with a relatively small number of lakes representing each FCT. Further work in this report on fish community effects excluded classification by FCT because of small sample size.

Trend-through-time data (i.e. serial data) analyses are appropriate for examination of community effects on lake trout yield, growth, and catch- or harvest-per-unit-area. However, such data sets are rare. As an alternative, analyses of data from a broad spectrum of lakes (i.e. spatial data) can be used to examine lake trout communities. We therefore compiled data sets consisting of: (1) angling creel data from a large set of Ontario lakes, to document yield and harvest-per-unit-effort (HUE); (2) gillnet catch and effort data from a second set of lakes, to represent estimates of lake trout relative abundance; (3) size and age specific lake trout growth data from lakes with different species compositions; and (4) fish size distribution data from a small set of lakes for analysis of fish particle size distribution. We then examined the degree to which the aquatic environment and the composition of the fish community (i.e. the assemblage of fishes present) affect the levels of relative abundance, yield and size of lake trout.

There were significant and large correlations in the data sets that confounded analysis (lake surface area versus gillnet and angling catch, lake surface area and harvesting effort). Lake area and effort had to be taken into account in the angling data, through the use of analysis of covariance (ANCOVA) or a randomized block design. A randomized block design involves partitioning the data into small blocks to isolate the effects of angling effort and lake area, followed by analysis of variance (ANOVA). Small sample sizes in many blocks precluded the use of this technique, thus for our analyses, we relied only on ANCOVA of angling and gillnet data, growth and production comparisons, and examination of fish size distribution.

To summarize, the data discussed in this report vary from extensive to intensive, each of which has its merits and shortcomings. We have taken a hierarchical approach in reporting our work. We first examined a large number of lakes (>1700) with presence-absence information on fish species, to determine whether FCTs differ in abiotic factors. We then considered fewer lakes (<150) for which detailed lake trout population data were available. For these lakes, we examined the variability in lake trout yield, relative abundance and size as related to FCT, environmental factors and fish community composition. Following this, a small number of lakes, with varying fish assemblages and for which intensive lake trout growth data were available, were examined for interactions between other fish species and lake trout. We also examined the Lake Opeongo lake trout growth and production data, before and after the introduction of lake herring (*Coregonus artedii*), to confirm trends found in the growth data set. Lastly, we examined fish particle size data in the general discussion.

EXAMINATION OF THE FISH COMMUNITY TYPE CLASSIFICATION

The presence of a particular fish assemblage is related to a number of different factors: natural and man-induced patterns of colonization and extinction; the environmental conditions present; and the physiological attributes of the fish species (McPhail and Lindsey 1970; Johnson et al. 1977; Hartman 1980; Tonn and Magnuson 1982; Marshall and Ryan 1987). To determine whether physico-chemical characteristics differed among fish community types, we obtained data from the Aquatic Habitat Inventory Data Base (AHIDB). Data were available for 1749 lake trout lakes (Table 1), which represents about 75% of the estimated 2318 lake trout lakes in Ontario. These lakes are distributed throughout Ontario (Martin and Olver 1976), and are subject to a variety of stresses (OMNR 1978). Fish community types represented by 10 or more lakes were included in the analysis.

In addition to the AHIDB, an angling data set was compiled to examine whether differences in lake trout yields could be detected among FCTs. This data set consisted of angler catch and effort data (Table 2), collected from 143 lakes across the province, with the majority of the lakes located in south-central Ontario. Each lake had experienced several years of moderate to intense fishing pressure. However, complete, long-term creel records were seldom available.

METHODS

Both correlation and gradient analyses (Whittaker 1967) were used to discern trends or patterns in the occurrence of various FCTs along gradients of lake surface area, mean and maximum depth, secchi disk transparency, conductivity, and morphoedaphic index (MEI) (Ryder 1965). A quantitative analysis using fish species abundance data as the dependent variable was not possible, because such data were not collected for most of the lakes in the AHIDB.

The most recent year recorded of annual catch and effort values for the angling data set were used. The yield data may not represent a sustainable yield from each lake, however, these were the best data available and we, therefore, proceeded with the analyses. Survey data from a single season were accepted as an annual estimate when angling was negligible at other times of the year. The comparison of yield among FCTs was carried out for FCTs represented by a minimum of eight lakes. Trends were detected by applying ANOVA, with differences in means determined through

Table 1. Summary of morphometric information on 1,749 Ontario lake trout lakes used in the present analysis.

Variable	No. of lakes	Minimum value	Mean	Maximum value
Area (ha)	1,749	1.8	629.0	34,807
Maximum depth (m)	1,748	2.1	33.7	2213.5
Mean depth (m)	1,744	1.3	10.9	47.5
Secchi disk (m)	1,720	0.5	5.3	22.0
MEI	1,697	0.2	4.3	48.6
Specific conductivity (μmho)	1,576	3.0	58.3	409.7

Table 2. Mean and range of variables included in angling creel data base used to examine the effect of environment and fish community on lake trout abundance, yield and size.

			Mean	Minimum	Maximum
Lake trout harvest measures	Total harvest	(Number)	855.56	2.80	13,283.00
		(kg)	970.78	5.20	20,949.00
	Harvest-per-unit-effort	(Number h^{-1})	0.17	0.02	1.83
		(kg h)	0.15	0.01	1.29
	Yield	(Number ha^{-1})	1.33	0.03	23.34
		(kg ha^{-1})	1.04	0.04	10.71
	Mean weight	(kg)	0.99	0.18	2.85
Effort measures	Total effort	(100 h)	8.43	0.06	92.27
	Effort per area	(h ha)	12.55	0.42	101.46
Abiotic variables	Lake area	(ha)	1,367.99	16.8	20,971.70
	Mean depth	(m)	15.37	5.6	47.50
	Maximum depth	(m)	47.98	17.7	162.80
	Volume >10m	$10^4 m^3$	17,060.69	40.1	435,146.00
	MEI		3.82	0.3	17.20
	Secchi	(m)	6.22	2.2	15.30
Community measures	# Major species		2.64	1.0	6.0
	# Additional predators		1.44	0.0	4.0
	Community complexity		0.50	0.0	1.0
			Presence (% of lakes)		
	Coregonines		63.2		
	Walleye		20.1		
	Burbot		41.7		
	Northern pike		36.1		
	Rainbow smelt		14.6		
	Walleye/pike		41.0		
	Walleye/burbot		47.9		
	Coregonines/smelt		64.6		

Duncan's multiple range test (Snedecor and Cochran 1980). This was followed by ANCOVA in which lake area and angler effort were the covariates.

RESULTS

Significant correlations between all environmental variables ($P < 0.05$) made it difficult to separate their individual effects and limited further analyses of the relationship between abiotic factors and FCT. Presentation of results of the gradient analysis is limited to two representative environmental variables. A plot of FCTs along lake area and MEI gradients showed a trend to increasing numbers of major species in larger lakes, and no clear trends in species occurrence with MEI (Fig. 1).

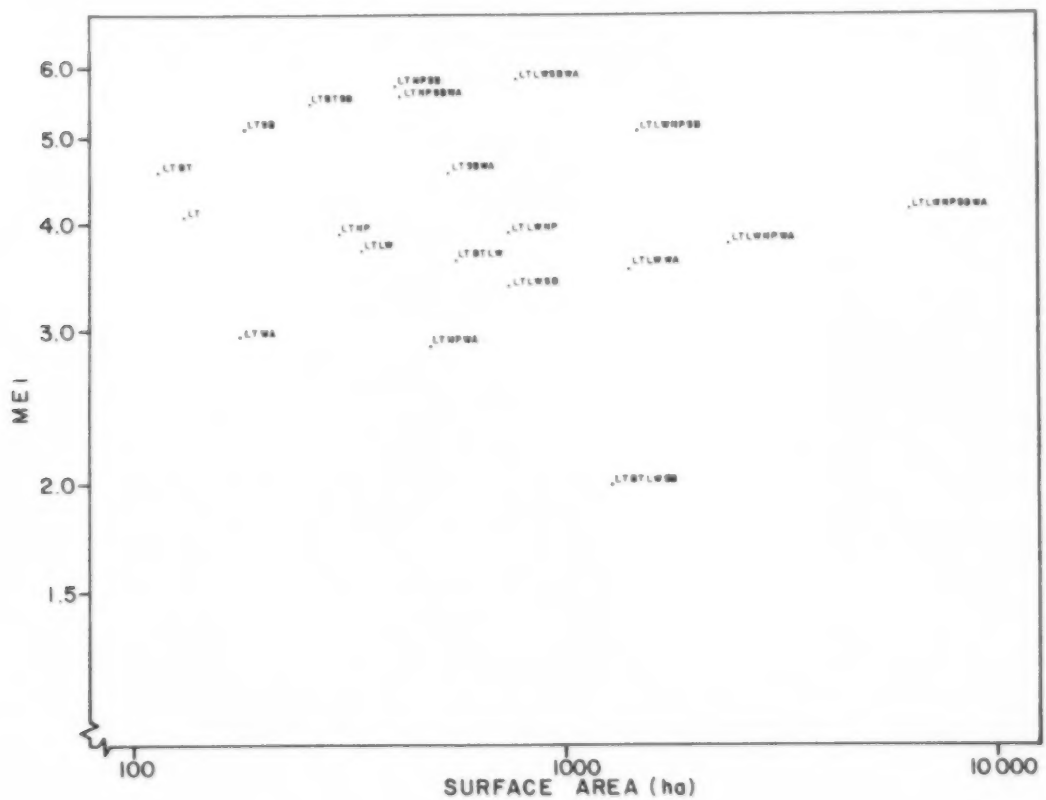


FIG. 1. Environmental conditions of lakes classed by FCT. Each FCT is represented by its mean along gradients of MEI and surface area. (LT = lake trout, BT = brook trout, NP = northern pike, SB = smallmouth bass, WA = walleye, LW = lake whitefish.)

Complete information was available for angling effort and catch data by number of fish for 87 lakes, and by weight of fish for 125 lakes. The mean lake trout angling yield appeared to vary greatly among FCTs represented by eight or more lakes (Fig. 2). An ANOVA ($\log_{10}$ transformed values) indicated that lake trout yield was significantly different among several FCTs (P <0.01). Duncan's multiple range test (Snedecor and Cochran 1980) indicated that the yield by number for FCT 18 (lake trout, smallmouth bass) was significantly higher than FCT 28 (lake trout, lake whitefish, northern pike), and that FCT 18 was significantly higher than FCT 28, 29 (FCT 28 and walleye), 31 (FCT 29 and smallmouth bass), and 48 (lake trout, brook trout) by weight. All other pair-wise comparisons of yields from other FCTs were not significantly different. As lakes with simple FCTs tended to be smaller in size than those with complex communities, we reanalysed the harvest data using ANCOVA, to compensate for the lake area and effort influence. This treatment demonstrated there were no significant differences in angling harvest due to FCT.

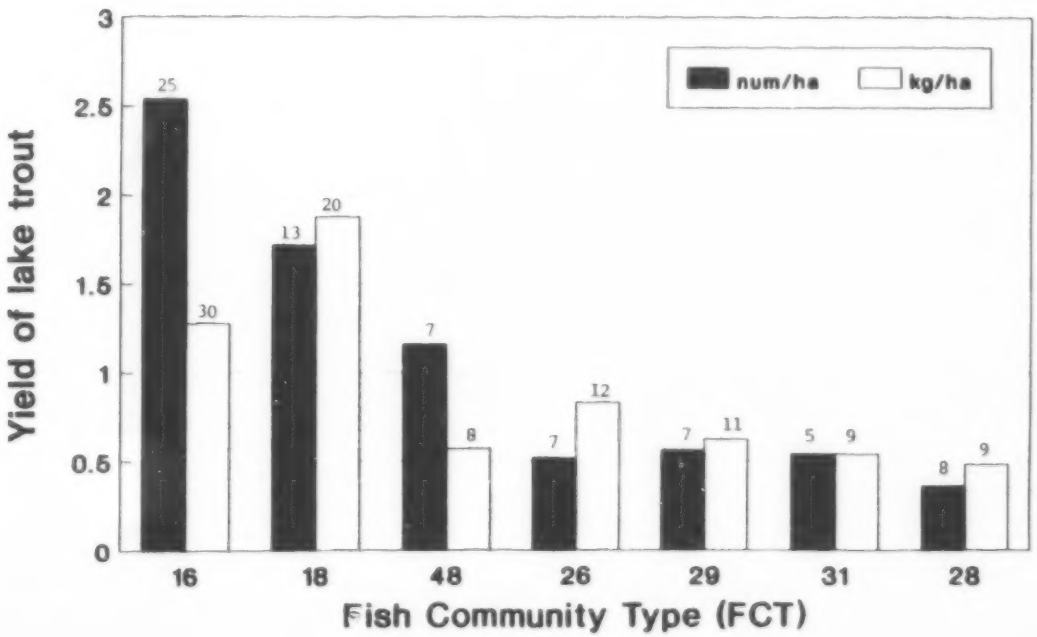


FIG. 2. Mean lake trout angling yield (numbers and weight) for lakes of differing FCTs. The sample size is noted by the number above each bar. Species representing each FCT are: 16 - lake trout; 18 - lake trout, smallmouth bass; 48 - lake trout, brook trout; 26 - lake trout, lake whitefish, smallmouth bass; 29 - lake trout, lake whitefish, walleye, northern pike; 31 -lake trout, lake whitefish, walleye, northern pike, smallmouth bass; 28 - lake trout, lake whitefish, northern pike.

DISCUSSION

The variation within each FCT was so great (low power; Parkinson et al. 1988) that FCTs could not be separated out in pair-wise comparisons using either the AHIDB or the angling data set. As well, using the ANCOVA, we were unable to detect significant differences in harvest among FCTs. The lack of clear definition of differences among FCTs, based on our analysis, is not surprising given the different patterns of natural and man-induced colonization and extinction in lakes throughout the province, and the small number of lakes representing some FCTs in the angling data base. In particular, the widespread and often unauthorized introductions of smallmouth bass, yellow perch (*Perca flavescens*), rainbow smelt (*Osmerus mordax*), crayfish, and lake herring have led to declines or shifts in native fish populations (Martin and Fry 1973; Evans and Waring 1987).

THE EFFECT OF ENVIRONMENT AND FISH COMMUNITY ON LAKE TROUT ABUNDANCE, YIELD AND SIZE

METHODS

Environmental and community effects on lake trout were examined using an angling data set and a gillnet data set. The angling data set (described in the previous section), and the gillnet data set described below, were used to examine the effect of environment and fish community on lake trout abundance, yield and size. The angling data set provided four dependent variables for analysis:

- total harvest of lake trout by number and by weight in kg;
- harvest-per-unit-effort (HUE) in number h^{-1} and kg h^{-1};
- yield of lake trout in number ha^{-1} and kg ha^{-1}; and
- mean lake trout weight (kg).

The effort expended by anglers is frequently expressed as rod-hours or angler-hours, which can mean different things, depending on the fishing season and characteristics of the fishery. We have selected total angler-hours as the most appropriate effort measure for these analyses, although we acknowledge that effort may be underestimated in instances where a substantial winter fishery exists.

The gillnet data set assembled was composed of catch and effort data for index gillnet surveys

from 76 lakes sampled as part of the lake inventory program in northwestern Ontario, research and assessment unit study lakes, and district lakes (Table 3). Minimum sampling requirements for inclusion in the data set were multiple overnight sets of standard gill net gangs (3.8-11.4 cm mesh stretched measure, in 1.3 cm increments) randomly set throughout each lake during the period of thermal stratification. The data set included lakes which varied widely in their suitability for lake trout, from those that would be considered to have marginal lake trout habitat, to those with excellent habitat. A 100 m length of gill net was used as the standard unit of effort. The gillnetting data set was assumed to have less size- and species-selection bias and better data on other fish species than the angling data set. Gillnet data were available for 66 lakes with lake trout catch recorded by number, and for 40 lakes with catch recorded by weight.

The gillnet data set provided four dependent variables for analysis:

- percent proportional abundance of lake trout in catch (lake trout catch/total catch)*100 in number and kg;
- catch-per-unit-effort (CUE) for lake trout in number 100 m^{-1} and kg 100 m^{-1};
- total CUE for all species combined in number 100 m^{-1} and kg 100 m^{-1}; and
- mean weight of lake trout in kg (total weight of lake trout caught/total number of lake trout caught).

The fish community was described for lakes in both data sets by independent variables grouped into two categories:

Category 1: Species richness or diversity

- Community complexity (see definition below);
- Number of major species; and
- Number of additional predators.

It was not possible to test for differences among FCTs because of small sample sizes for many FCTs; instead, an index of community complexity was used. This index was calculated using the same six species used in the FCT classification scheme (brook trout, lake trout, lake whitefish, northern pike, smallmouth bass and walleye). Simple communities (community complexity = 0) were those where lake trout occurred alone or with one other of the above species. Complex communities (community complexity = 1) were those where lake trout occurred with two or more of these species. The number of additional predators indicates the number of the following species present: walleye, northern pike, burbot (*Lota lota*), and smallmouth bass.

Table 3. Mean and range of variables included in gillnet data base used to examine the effect of environment and fish community composition on lake trout abundance, yield and size.

			Mean	Minimum	Maximum
Harvest variables	Lake Trout Proportional abundance	(% number)	15.07	0.27	86.67
		(% wt)	24.93	0.98	86.87
	Lake trout catch-per-unit-effort	(number 100 m^{-1})	2.36	0.09	14.25
		(kg 100 m^{-1})	3.62	0.19	20.73
	All species CUE	(number 100 m^{-1})	25.04	1.72	326.17
		(kg 100 m^{-1})	18.42	2.98	109.68
	Lake trout mean weight	(kg)	1.58	0.25	4.2
Effort measure	Total effort	(100 m sets)	34.78	1.12	550.58
Abiotic Variables	Lake area	(ha)	2,838.03	38.9	64,725.00
	Mean depth	(m)	14.03	4.9	47.5
	Maximum depth	(m)	46.01	15.6	162.80
	Volume >10 m	$10^4 m^3$	22,141.93	74.8	272,662.60
	MEI		3.07	0.3	16.40
	Secchi	(m)	5.82	2.1	10.40
Community attributes	# Major species		2.75	1.0	5.0
	# Additional predators		1.20	0.0	4.0
	Community complexity		.58	0.0	1.0
			Presence (% of lakes)		
	Walleye		23.7		
	Burbot		46.1		
	Northern pike		34.2		
	Lake whitefish		53.9		
	Lake herring		40.8		
	Coregonines		67.1		
	Rainbow smelt		1.3		
	Smallmouth bass		15.8		
	Yellow perch		46.1		
	Walleye/pike		43.4		
	Walleye/burbot		52.6		
	Coregonines/smelt		67.1		

Category 2: Presence/absence of select species or taxonomic groups which represent potential prey for, predators on, or competitors with lake trout.

- Walleye;
- Burbot;
- Northern pike;
- Rainbow smelt;
- Lake whitefish (gillnet data set only);
- Lake herring (gillnet data set only);
- Coregonines (lake whitefish, round whitefish (*Prosopium cylindraceum*) and/or lake herring;
- Walleye and/or northern pike;
- Walleye and/or burbot; and
- Coregonines and/or rainbow smelt

An analysis of the effect of fish community composition on lake trout catch cannot be carried out without considering the effects of major catch correlates, such as fishing effort and lake size, and other physical parameters that describe lake trout habitat or lake productivity. Therefore, a second set of independent variables were compiled for analysis as follows (Tables 2 and 3):

- Total effort (angler-hrs or 100 m of gill net);
- Relative effort (angler-hrs ha^{-1} or 100 m of gill net ha^{-1});
- Lake area (ha);
- Mean depth (m);
- Maximum depth (m);
- Volume of water greater than 10 m deep ($m^3 \times 10^4$);
- Morphoedaphic index (MEI); and
- Secchi depth (m).

The effects of the fish community composition and abiotic variables on lake trout catch and harvest were determined through correlation analysis, ANOVA and ANCOVA. It is acknowledged that many of the correlation results may have no statistical validity, due to significant auto-correlation among the independent variables.

Data for continuous variables were first examined for normality using the Shapiro-Wilk statistic (Shapiro and Wilk 1965). Log_{10} transformations were applied to normalize the variables prior to data analyses. This transformation was more effective in reducing the asymmetry of the variable

distributions than other transformations such as $\log_e$ and square root. Interval level data (community complexity, number of major species, number of predators, and presence/absence of species or taxonomic groups) were not transformed.

RESULTS

The variables affecting angling harvest of lake trout, and the strength of these relationships were initially examined through the following simple correlation analyses:

- Lake trout harvest measures versus angling effort and abiotic variables (Table 4);
- Lake trout harvest measures versus fish community composition (Table 5); and
- Fish community composition versus angling effort and abiotic variables (Table 6).

Effort accounted for 79% by number and 72% by weight of the variability (r^2) in the total angling harvest of lake trout (Table 4). The volume of water greater than 10 m deep, mean depth, and maximum depth were all highly correlated with total harvest (Table 4) and with each other. These parameters were related to lake size, with lake area itself accounting for 46% and 49% of lake trout harvest variability by numbers and weight, respectively (Table 4). Total harvest was positively correlated with most measures of fish community composition (Table 5).

While not related to lake size directly, angling HUE (weight) was positively related to the mean depth and volume measurement, and negatively related to MEI, total effort, and relative fishing effort (Table 4). Small but significant correlations existed between HUE (weight) and the presence of coregonines, coregonines and/or smelt, and northern pike (Table 5).

Lake area was negatively correlated with angling yield by number and weight (Table 4), while positive correlations of yield existed with total effort and relative fishing effort (Table 4). Lake trout yield was negatively correlated with almost every measure of community structure (Table 5). Especially important was the presence of coregonines, walleye, burbot, or both walleye and burbot, and the number of major species. Most measures of community structure were correlated with angling effort and abiotic variables (Table 6).

The differences in angling harvest by weight, related to community composition, were not significant when ANCOVA, which controls for the effects of angling effort and lake area, was used (Table 7). Annual harvest of lake trout by number, however, was positively influenced by the presence of coregonines. The presence of the group coregonines and/or smelt also affected the

Table 4. Correlation matrix showing r^2 values of lake trout catch descriptors from the angling creel versus effort measures and the abiotic variables. A single asterisk indicates a significance level of $P < .05$; a double asterisk $P < .01$; - sign indicates negative relationship, no sign indicates positive relationship or no relationship in the case of 0 . The bracketed number indicates the sample size.

	Total harvest		Harvest-per-effort		Yield		Mean weight
	(No)	(kg)	(No/h)	(kg/h)	(No/ha)	(kg/ha/yr)	(kg)
Total effort	0.79** (87)	0.72** (125)	-0.07* (87)	-0.06** (125)	0.09** (87)	0.18** (125)	0.05* (86)
Relative effort	0.01 (87)	0.00 (125)	-0.04* (87)	-0.23** (125)	0.59** (87)	0.48** (125)	-0.13** (86)
Lake area	0.46** (98)	0.49** (143)	-0.01 (87)	-0.03 (125)	-0.10** (98)	-0.07** (143)	0.21** (97)
Mean depth	0.13** (97)	0.18** (142)	0.01 (86)	0.06** (124)	0.00 (97)	0.01 (142)	0.08** (96)
Max. depth	0.27** (98)	0.26** (143)	0.03 (87)	-0.07** (125)	0.00 (98)	0.00 (143)	0.05* (97)
Vol. >10 m	0.41** (82)	0.53** (114)	0.00 (75)	0.06** (105)	-0.12 (82)	-0.03 (114)	0.22** (82)
MEI	0.00 (96)	0.00 (141)	-0.08** (85)	-0.05* (123)	0.02 (96)	0.02 (141)	0.00 (95)
Secchi depth	0.02 (97)	0.02 (142)	0.00 (87)	0.00 (125)	-0.09** (97)	0.08** (142)	-0.01 (96)

Table 5. Correlation matrix showing r^2 values of lake trout catch descriptors from the angling creel versus fish community attributes. A single asterisk indicates a significance level of $P < .05$; a double asterisk $P < .01$; - sign indicates negative relationship, no sign indicates positive relationship or no relationship in the case of 0. The bracketed number indicates the sample size.

	Total harvest		Harvest-per-effort		Yield		Mean weight
	(No)	(kg)	(No/h)	(kg/h)	(No/ha)	(kg/ha)	(kg)
P/A coregonines	0.12** (98)	0.10** (143)	0.04 (87)	0.05* (125)	-0.07* (98)	-0.05** (143)	0.18** (97)
P/A walleye	0.08** (98)	0.05** (143)	-0.01 (87)	0.00 (125)	-0.05* (98)	-0.08** (143)	0.08** (97)
P/A burbot	0.04 (98)	0.09** (143)	0.00 (87)	0.03 (125)	-0.07** (98)	-0.01 (143)	0.17** (97)
P/A northern pike	0.06* (98)	0.06** (143)	0.00 (87)	0.04* (125)	-0.05* (98)	-0.04* (143)	0.15** (97)
P/A rainbow smelt	0.07** (98)	0.12** (143)	-0.02 (87)	0.00 (125)	0.00 (98)	0.01 (143)	0.07** (97)
Walleye-pike	0.05* (98)	0.06** (143)	-0.01 (87)	0.01 (125)	-0.07** (98)	-0.06** (143)	0.18** (97)
Walleye-burbot	0.05* (98)	0.08** (143)	0.00 (87)	0.02 (125)	-0.10** (98)	-0.07** (143)	0.15** (97)
Coregonines smelt	0.12** (98)	0.11** (143)	0.04 (87)	0.05* (125)	-0.06* (98)	-0.05** (143)	0.20** (97)
# major species	0.15** (98)	0.20** (143)	-0.07* (87)	0.00 (125)	-0.09** (98)	-0.05** (143)	0.21** (97)
# additional predators	0.14** (98)	0.20** (143)	-0.04 (87)	0.00 (125)	-0.06* (98)	-0.03* (143)	0.20** (97)
Community complexity	0.10** (98)	0.17** (143)	-0.06* (87)	0.00 (125)	-0.07** (98)	-0.03* (143)	0.20** (97)

Table 6. Correlation matrix showing r^2 values of fish community attributes from the angling creel versus abiotic variables. A single asterisk indicates $P < .05$; a double asterisk $P < .01$; - sign indicates a negative relationhip, no sign indicates positive relationship or no relationship in the case of 0. The bracketed number indicates the sample size.

	Presence/absence										
	Coregonines	Walleye	Burbot	Northern pike	Rainbow smelt	Walleye /pike	Walleye /burbot	Coregonines /smelt	No. major species	No. additional predators	Community complexity
Total effort	0.07** (126)	0.07** (126)	0.05** (126)	0.04* (126)	0.15** (126)	0.05** (126)	0.05* (126)	0.07** (126)	0.27** (126)	0.23** (126)	0.18** (126)
Relative effort	-0.14** (126)	-0.06** (126)	-0.07** (126)	-0.06** (126)	0.00 (126)	-0.08** (126)	-0.11** (126)	-0.14** (126)	-0.05* (126)	-0.05* (126)	-0.04* (126)
Lake area	0.31** (144)	0.25** (144)	0.16** (144)	0.19** (144)	0.10** (144)	0.23** (144)	0.24** (144)	0.30** (144)	0.45** (144)	0.40** (144)	0.32** (144)
Mean depth	0.08** (143)	0.01 (143)	0.04* (143)	0.00 (143)	0.06** (143)	0.02 (143)	0.06** (143)	0.09** (143)	0.04* (143)	0.04* (143)	0.06** (143)
Maximum depth	0.10** (144)	0.05** (144)	0.08** (144)	0.04* (144)	0.06** (144)	0.06** (144)	0.08** (144)	0.12** (144)	0.10** (144)	0.10** (144)	0.07** (144)
Volume >10 m	0.27** (114)	0.21** (114)	0.21** (114)	0.14** (114)	0.15** (114)	0.18** (114)	0.26** (114)	0.27** (114)	0.40** (114)	0.36** (114)	0.32** (114)
MEI	0.00 (142)	0.00 (142)	-0.04* (142)	0.02 (142)	-0.01 (142)	0.02 (142)	-0.02 (142)	-0.01 (142)	0.01 (142)	0.01 (142)	0.00 (142)
Secchi depth	-0.01 (143)	0.00 (143)	0.00 (143)	-0.06** (143)	0.00 (143)	-0.04* (143)	0.00 (143)	-0.01 (143)	0.00 (143)	0.01 (143)	0.00 (143)

Table 7. Explained variance (r^2) in lake trout total angling harvest (number and weight) indicated by analysis of covariance of community composition controlling for the effects of total effort and lake area. r^2 values for effort and area alone are recorded below for reference. A single asterisk indicates the F value for the community variable was significant at $P < .05$ and a double asterisk at $P < .01$, otherwise there was no significant difference between class means for the variables. A - sign indicates a negative relationship and no sign indicates a positive relationship or no relationship in the case of 0.

		Lake trout total harvest	
		(No yr^{-1})	(kg yr^{-1})
Fish community type	Existing FCT	-0.04	-0.03
Species richness	Community complexity	-0.01*	0.00
	# major species	-0.03*	-0.01
	# additional predators	-0.01*	0.00
Presence or absence of species (groups)	Walleye	0.00	0.00
	Burbot	0.00	0.00
	Northern pike	0.00	0.00
	Rainbow smelt	0.00	0.00
	Coregonines	0.01*	0.00
	Walleye-pike	0.00	0.00
	Walleye-burbot	0.00	0.00
	Coregonines-smelt	0.01*	0.00
	Effort and surface area	0.80	0.78

annual harvest but, as is apparent by the small r^2 value, this was entirely due to the contribution of the coregonines and not the smelt. Species richness and the index of community complexity had a significant effect on harvest, with greater numbers of lake trout caught in lakes with simpler fish communities (those with 0 or 1 major species present in addition to lake trout). In general, the significant r^2 values were much smaller than the r^2 due to effort and surface area alone. This indicates that, even where significant, the effects of community attributes were negligible compared to the effect of lake area and angling effort.

A series of correlation matrices were produced for the gillnet data, to illustrate trends and allow comparison with the angling data set. As with the angling data, the following correlations were examined:

- CUE versus the abiotic variables (Table 8);
- CUE versus community attributes (Table 9); and
- Community attributes versus abiotic variables (Table 10).

Table 8. Correlation matrix showing r^2 values of gillnet catch descriptors versus effort and the abiotic variables. A single asterisk indicates a significance level of $P < .05$; a double asterisk $P < .01$; - sign indicates negative relationship, no sign indicates positive relationship or no relationship in the case of 0. The bracketed number indicates the sample size.

	Lake trout		Lake trout		All species		Lake trout
	% proportional abundance		CUE		CUE		Mean weight
	(no)	(kg)	(no/100 m)	(kg/100 m)	(no/100 m)	(kg/100 m)	(kg)
Total effort	-0.01	-0.01	-0.08*	-0.02	-0.04	0.00	0.05
	(66)	(40)	(66)	(40)	(66)	(40)	(40)
Lake area	-0.03	-0.10*	-0.01	-0.11*	0.06	0.00	0.28**
	(73)	(40)	(63)	(38)	(63)	(38)	(40)
Mean depth	0.11**	0.12*	0.06	0.03	-0.03	-0.15*	0.02
	(73)	(40)	(63)	(38)	(63)	(38)	(40)
Maximum depth	0.04	0.01	0.02	-0.03	-0.01	-0.24**	0.03
	(73)	(40)	(63)	(38)	(63)	(38)	(40)
Volume >10 m	0.00	0.00	0.00	-0.05	0.00	-0.06	0.12
	(54)	(32)	(46)	(30)	(46)	(30)	(32)
MEI	-0.13**	-0.18**	-0.01	-0.01	0.18**	0.38**	0.01
	(72)	(40)	(62)	(38)	(62)	(38)	(40)
Secchi depth	0.18**	0.18**	0.07*	0.04	-0.14**	-0.14*	-0.18**
	(73)	(40)	(63)	(38)	(63)	(38)	(40)

Table 9. Correlation matrix showing r^2 values of gillnet catch descriptors versus fish community attributes. A single asterisk indicates a significance level of $P < .05$; a double asterisk $P < .01$; - sign indicates negative relationship, no sign indicates positive relationship or no relationship in the case of 0. The bracketed number indicates the sample size.

	Lake trout		Lake trout		All species		Lake trout
	% proportional abundance		CUE		CUE		Mean weight
	(no)	(kg)	(no 100 m^{-1})	(kg 100 m^{-1})	(no 100 m^{-1})	(kg 100 m^{-1})	(kg)
P/A coregonines	-0.03 (76)	-0.07 (42)	-0.07* (66)	-0.06 (40)	0.04 (66)	0.01 (40)	0.36** (42)
P/A walleye	-0.11** (76)	-0.34** (42)	-0.06 (66)	-0.18** (40)	0.10** (66)	0.10* (40)	0.14* (42)
P/A burbot	-0.04 (76)	-0.14* (42)	-0.10* (66)	-0.24** (40)	0.00 (66)	-0.03 (40)	0.08 (42)
P/A northern pike	-0.01 (76)	-0.13* (42)	-0.05 (66)	-0.24** (40)	0.00 (66)	-0.01 (40)	0.10* (42)
P/A. rainbow smelt	0.00 (76)	- (42)	- (66)	- (40)	- (66)	- (40)	- (42)
Walleye-pike	-0.02 (76)	-0.18** (42)	-0.02 (66)	-0.18** (40)	0.04 (66)	0.01 (40)	0.15* (42)
Walleye-burbot	-0.07* (76)	-0.20** (42)	-0.10* (66)	-0.20** (40)	0.01 (66)	0.00 (40)	0.27** (42)
Coregonines-smelt	-0.03 (76)	-0.07 (42)	-0.07* (66)	-0.06 (40)	0.04 (66)	0.01 (40)	0.36** (42)
No. major species	-0.14** (76)	-0.37** (42)	-0.09* (66)	-0.17** (40)	0.12** (66)	0.14* (40)	0.40** (42)
No. additional predators	-0.11** (76)	-0.49** (42)	-0.13** (66)	-0.45** (40)	0.03 (66)	0.02 (40)	0.23** (42)
Community complexity	-0.04 (76)	-0.10* (42)	-0.04 (66)	-0.05 (40)	0.01 (66)	0.01 (40)	0.44** (42)

Table 10. Correlation matrix showing r^2 values of fish community attributes versus abiotic variables from gillnet catches. A single asterisk indicates a significance level of $P < .05$; a double asterisk $P < .01$; - sign indicates negative relationship, no sign indicates positive relationship or no relationship in the case of 0. The bracketed number indicates the sample size.

	Presence/absence										
	Coregonines	Walleye	Burbot	Northern pike	Rainbow smelt	Walleye /pike	Walleye /burbot	Coregonines /smelt	No. major species	No. additional predators	Community complexity
Total effort	0.04 (66)	0.00 (66)	0.03 (66)	0.00 (66)	- (66)	0.00 (66)	0.00 (66)	0.04 (66)	0.03 (66)	0.00 (66)	0.05 (66)
Lake area	0.34** (73)	0.25** (73)	0.18** (73)	0.21** (73)	0.00 (73)	0.37** (73)	0.20** (73)	0.34** (73)	0.40** (73)	0.36** (73)	0.40** (73)
Mean depth	0.05 (73)	0.00 (73)	0.07* (73)	0.00 (73)	0.03 (73)	0.00 (73)	0.04 (73)	0.05 (73)	0.00 (73)	0.01 (73)	0.02 (73)
Maximum depth	0.14** (73)	0.03 (73)	0.20** (73)	0.06* (73)	0.01 (73)	0.07* (73)	0.14** (73)	0.14** (73)	0.08* (73)	0.14** (73)	0.12** (73)
Volume >10 m	0.27** (54)	0.18** (54)	0.16** (54)	0.10* (54)	0.01 (54)	0.23** (54)	0.14** (54)	0.27** (54)	0.27** (54)	0.26** (54)	0.32** (54)
MEI	0.01 (72)	0.03 (72)	0.00 (72)	0.05 (72)	-0.02 (72)	0.10** (72)	0.00 (72)	0.01 (72)	0.12** (72)	0.05 (72)	0.04 (72)
Secchi depth	-0.04 (73)	-0.14** (73)	0.00 (73)	-0.07* (73)	-0.02 (73)	-0.12** (73)	-0.02 (73)	-0.04 (73)	-0.13** (73)	-0.07 (73)	-0.05 (73)

Total species CUE by weight was negatively correlated with mean and maximum depth (Table 8). The CUE (number 100 m^{-1} and kg 100 m^{-1}) summed for all species in the catch was positively correlated with the number of major species, the presence of walleye and MEI, and negatively correlated with secchi depth (Table 8 and 9). However, most community variables were positively correlated with lake area (Table 10). This suggests, as in the angling discussion data, that the community and area effects cannot be separated with correlation analysis. In general, the total CUE (all species) in lake trout lakes appeared to be higher in shallow lakes with low secchi readings and high MEI that contained walleye and other major species.

Abundance of lake trout (CUE by number) was positively correlated with secchi depth and negatively correlated with total effort, and CUE (by weight) was negatively related to lake area (Table 8), again making it impossible to separate out different effects.

The relative abundance of lake trout measured by gillnet CUE was strongly correlated with many of the indices of community composition (Table 9). Lake trout CUE (weight) was strongly negatively correlated with the presence of walleye, burbot, northern pike, and the groups walleye/pike and walleye/burbot (Table 9). Lake trout CUE (numbers) was negatively correlated with the presence of burbot and coregonines (Table 9). Strong negative correlations of lake trout CUE were apparent with both the number of major species and the number of predators, most likely due to the effect of walleye, burbot, and pike (Table 9). In overview, **the greatest lake trout CUE occurred in small, transparent lakes with few predator species or other major species.**

The proportional abundance of lake trout in the gillnet catch was similar to lake trout gillnet CUE in its correlation with the community and abiotic variables (Tables 8 and 9). However, it was also negatively related to MEI and positively related to mean depth. The gillnet analysis, therefore, suggest that **lake trout reach their greatest proportional abundances in small, deep, low MEI lakes, with highly transparent water and simple fish communities.**

As with the angling data, the mean weight of lake trout in the gillnet catch was greatest in large lakes (Table 8). In addition, mean weight was negatively associated with lakes with high secchi depth readings (Table 8).

The results of the ANCOVA for the gillnet data, in which lake area was the covariate, are summarized in Table 11. Burbot and northern pike negatively affected lake trout CUE (weight) and coregonids negatively affected lake trout CUE (number). More significantly, the total number of predators present was negatively correlated with lake trout CUE, explaining 47% of the variance by weight and 18% by number.

Table 11. Explained variance (r^2) in lake trout gillnet CUE indicated by analysis of covariance of community composition controlling for the effects of lake area. r^2 value for area alone is recorded below for reference. A single asterisk indicates the F value for the community variable was significant at $P < .05$ and a double asterisk at $P < .01$, otherwise there was no significant difference between class means for the variables. A - sign indicates a negative relationship and no sign indicates a positive relationship or no relationship in the case of 0.

		Lake trout CUE	
		(No./100 m)	(kg/100 m)
Species richness	Community complexity	-0.03	0.00
	No. major species	-0.10	-0.16
	No. additional predators	-0.18*	-0.47**
Presence or absence of species (groups)	Walleye	-0.02	-0.06
	Burbot	-0.06	-0.10*
	Northern pike	-0.01	-0.14*
	Yellow perch	0.00	0.02
	Lake herring	-0.01	-0.01
	Lake whitefish	0.00	-0.02
	Coregonines	-0.07*	-0.01
	Walleye-pike	0.00	-0.06
	Walleye-burbot	-0.06	-0.07
	Lake surface area alone	-0.013	-0.11*

DISCUSSION

We found that lake area accounted for about half of the variation in the total harvest of lake trout by anglers (simple correlation analysis, Table 4). This is considerably lower than that reported by Goddard et al. (1987), who examined 87 lakes in Ontario and found that lake area explained 72% of the variance in the harvest of lake trout in Ontario lakes. Their lakes, however, were more uniform in harvest than those included in this analysis and this may have contributed to their higher correlation between harvest and lake area.

The 72% of the variation (r^2) in harvest weight of lake trout explained by angling effort in our analysis is similar to the 72% described by Schlesinger and McCombie (1983), and the 73% described by Goddard et al. (1987) in earlier analyses of Ontario lakes. This is not surprising, as many of the lakes are common to all three data sets.

As angling effort and lake area are the two major determinants of total harvest, Goddard et al. (1987) selected analysis of covariance as the basic tool for detecting variation in lake trout harvest attributable to differences in fish community structure. They noted an absence of significant differences among community groupings when the influence of effort and lake size was controlled. In a duplication of their analysis, using angling harvest as the dependent variable, we detected very small differences related to community composition that were overshadowed by the effects of lake area and angler effort. Given results from both analyses, it appears that **angling data do not allow a valid test of community effects because of the strong correlation between harvest, angler effort and lake surface area.**

The gillnet CUE data were considered more appropriate to test for community effects than the angling data set, because the correlation between angling effort and the catch variables was not present. However, it appears that in lakes that were less intensively gillnetted, more fish were captured per net set than in lakes with more frequent netting. This suggests that the nets were not all randomly placed, that effort was adjusted based on catch, or that the sampling had an impact on the numbers present. However, the variation in CUE by number explained by netting effort was low (r^2 = 0.08) and not significant for CUE by weight (Table 8). Therefore, the bias in the data set was small.

The gillnet ANCOVA (Table 11) indicated that coregonines had a significant negative effect (r^2 = 0.07) on lake trout relative abundance (CUE by number), independent of lake surface area. It also appeared that in lakes containing burbot and northern pike, and possibly other predators, lake trout abundance (CUE by weight) may have been lower due to predation and/or competition. **This is the first time a large portion of the variation in relative abundance (r^2 = 0.47) of a valuable sport fish has been explained by the presence of burbot, pike or other predators.**

LAKE TROUT GROWTH AND PRODUCTION IN RELATION TO FISH COMMUNITY COMPOSITION

Based on data from a number of Algonquin Park lakes, Martin (1952, 1966) suggested that growth parameters could be used as indicators of fish community effects. These papers showed that the average size and growth rate of lake trout depended upon the amount of fish or plankton in the diet. Those populations which had fish available as forage exhibited more rapid growth and

reached larger size. We considered the bioenergetic basis of these observations and fish community effects through analysis of growth efficiency (Paloheimo and Dickie 1966; Kerr and Martin 1970; Kerr 1971a, b; Kerr and Ryder 1977).

Relative growth efficiencies, known as *K*-lines in which a larger *K* value indicates a higher growth efficiency, were calculated for lake trout caught during four time periods in Lake Opeongo between 1937 and 1959, and for 22 additional lake trout populations for which data were available for a shorter time period. The *K*-lines from Lake Opeongo were based on weight-at-age data from the angling catch, before and after the lake herring introductions in 1944 and 1948. Growth efficiencies for other lakes were calculated, where possible, from multimesh gillnet survey data collected over several years.

In order to corroborate the *K*-line analysis, and further elucidate trends concerning prey species, age specific production and instantaneous growth rate (G), for Lake Opeongo lake trout before and after the lake herring introductions, were also examined (Carl et al. in press).

METHODS

Creel survey data or gillnet data from a single year were used if multi-year gillnet data were not available. The weight increment (ΔW) for a year of growth was the difference between the average weight for the next older age group (Wt + 1) and the average weight for the current age group (Wt). Growth efficiencies were estimated using these data and the formula described by Kerr and Ryder (1977):

$$\text{Relative } K = \Delta W / (W_t^{0.85} + \Delta W)$$

where W_t = initial body weight; and

ΔW = annual growth increment.

Analyses were restricted to age groups for which there were at least nine fish. Data were frequently available for lakes where the limited range of ages and small numbers of samples for each age group prevented analysis as described above. In these instances, data were entered into a length-based von Bertalanffy model, and length and weight-at-age were estimated. Only the general growth patterns rather than complete *K*-lines were described for lakes with insufficient data.

RESULTS

The *K*-line data from Lake Opeongo for the period 1937-43 show the pattern of relative growth efficiency before the first stocking of lake herring (Fig. 3). As fish grew in size (1937-1943), *K* declined from approximately 0.6 to 0.2, over the range of fish size of 0.4 kg to 1.30 kg. There was a rapid increase in *K* for fish over 1.30 kg in weight. The next three *K*-lines (1944-48, 1949-53, and 1954-59) show progressive improvement in the growth efficiency of lake trout over 0.70 kg in weight to a point where there was no "growth depression" evident in the 1954-59 data.

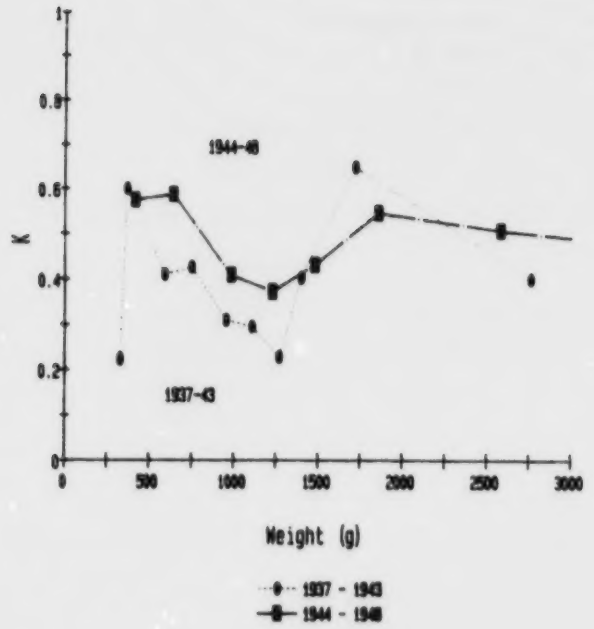
Lake Opeongo lake trout production responded in a similar manner. The production of age 4-10 yr fish increased almost 3-fold from the 1940s to the 1960-82 period (Table 12). The greatest absolute change occurred in age 7 and 8 fish, in which annual production increased from 361.3 kg to 873.0 kg and 93.4 kg to 747.4 kg, respectively (Table 12). The instantaneous growth efficiency (G) of age 7 and 8 fish increased, while efficiency declined for the age 11 fish (Table 13).

Inspection of the relative growth efficiency (*K*-line) graphs from 22 lake trout lakes indicated two possible groups. The first group exhibited *K*-lines that declined with weight relatively smoothly (Fig. 4-6). Populations exhibiting this pattern could further be categorized by the apparent maximum size (W_{MAX}) of fish that they could produce into three types: maximum size less than 2.0 kg (Fig. 4); maximum size greater than 2.0 kg but less than 3.0 kg (Fig. 5); and maximum size greater than 4.0 kg (Fig. 6). A second group of lakes exhibited irregular *K*-lines (Fig. 7).

The first type of lake (Fig. 4, sharp decline in *K*, W_{MAX}, 1.0-2.0 kg) is relatively small (less than 1000 ha), and does not contain coregonines. An exception is Lake Lavieille, which is 2402 ha in area and contains both lake herring and lake whitefish.

The second type of lake (Fig. 5, moderate decline in *K*, W_{MAX}, 2.0-3.0 kg) overlaps in surface area with the first type (412-6059 ha), but differs consistently in having both lake whitefish and lake herring present. The northwestern Ontario lakes contain one or more warm-coolwater species (smallmouth bass, northern pike and/or walleye). The southern Ontario lakes in the group contain brook trout.

The third type of lake (Fig. 6, slow decline in *K*, large W_{MAX}) varies considerably in size from 240 to 12,215 ha. Two of the lakes have rainbow smelt populations, four have lake whitefish and



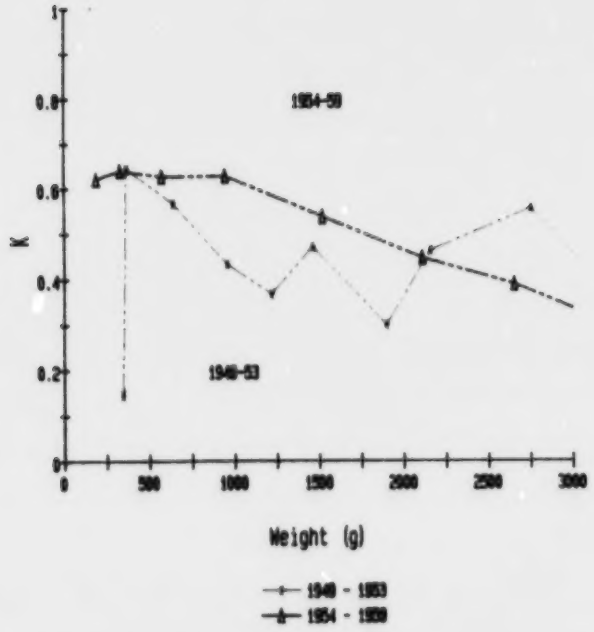


FIG. 3. Relationship between relative growth efficiency (K) and weight for lake trout for four different time periods in the history of Lake Opeongo. Data points correspond with annual growth increments.

Table 12. Mean age specific production (kg) for Lake Opeongo lake trout for the time periods 1940 to 1950, 1951 to 1959, and 1960 to 1982 from Carl et al. (in press).

	Production					
Total	1940-50	% of total	1951-59	% of total	1960-82	% of total
4**	178.8	12.2	220.8	9.0	341.1	8.4
5**	267.3	18.3	401.3	16.5	524.9	12.9
6**	377.2	25.8	437.8	18.0	644.5	15.9
7**	361.3	24.8	585.0	24.0	873.0	21.5
8**	93.4	6.4	323.5	13.3	747.4	18.4
9**	67.5	4.6	232.7	9.5	387.2	9.6
10**	25.1	1.7	76.8	3.1	296.2	7.3
11	62.5	4.3	115.0	4.7	139.6	3.4
12	27.8	1.9	45.8	1.9	106.1	2.6
Total	1460.9		2438.7		4060.0	

**Significant difference among means at $P = 0.01$.

Table 13. Mean age specific growth efficiency (P/B) for Lake Opeongo lake trout during the periods 1940 to 1950, 1951 to 1959 and 1960 to 1982, from Carl et al. (in press).

	Growth efficiency		
Age	1940-1950	1951-1959	1960-1982
4	0.81	0.85	0.90
5	0.67	0.77	0.73
6	0.59	0.56	0.59
7**	0.46	0.60	0.58
8**	0.14	0.34	0.38
9	0.16	0.33	0.22
10	0.17	0.14	0.23
11**	0.52	0.38	0.09
12	0.23	0.21	0.15

**Significant difference among means at $P = 0.01$.

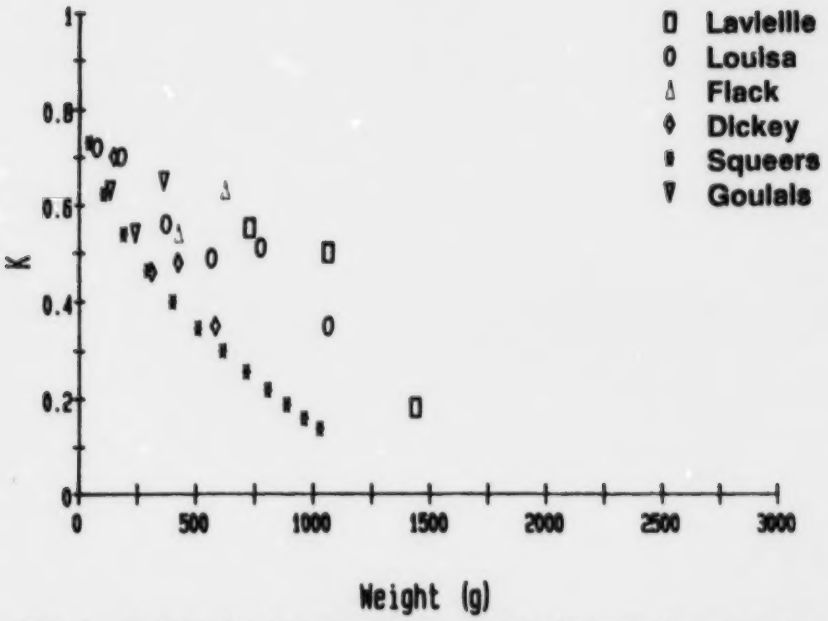


FIG. 4. Relationship between relative growth efficiency (K) and body weight for lake trout from a select set of lakes. Data points correspond with annual growth increments.

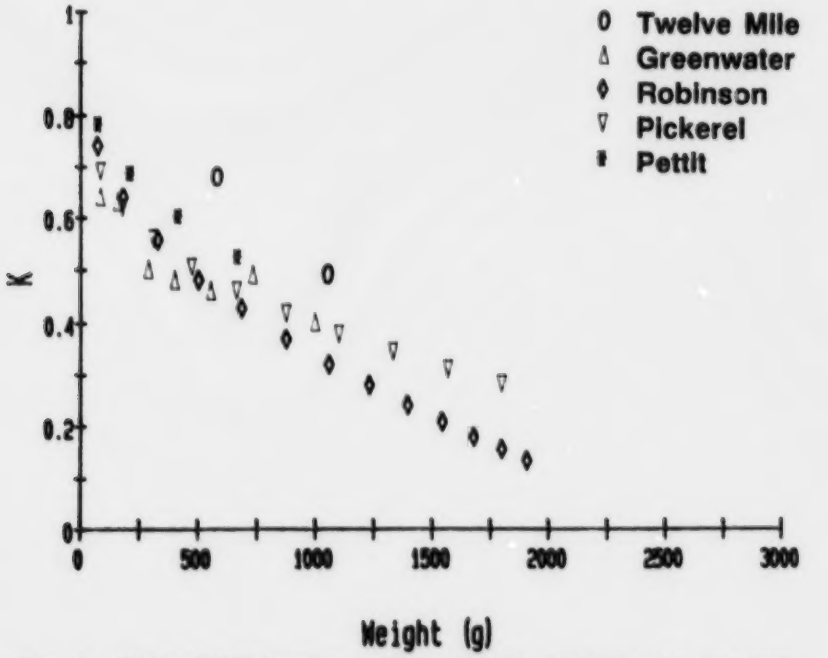


FIG. 5. Relationship between relative growth efficiency (K) and body weight for lake trout from a select set of lakes. Data points correspond with annual growth increments.

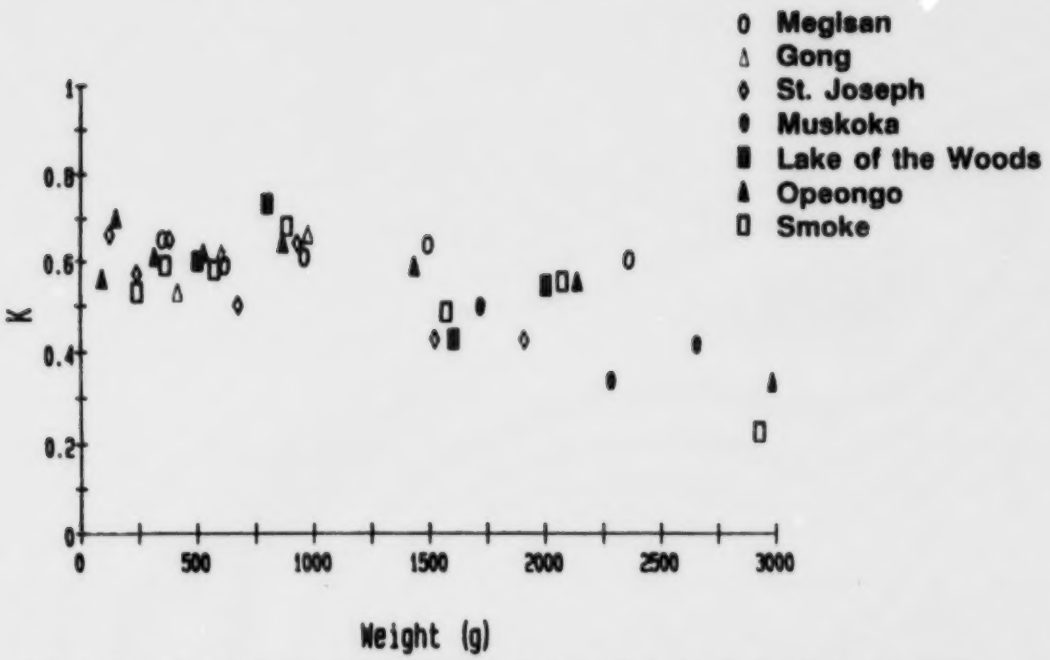


FIG. 6. Relationship between relative growth efficiency (K) and body weight for lake trout from a select set of lakes. Data points correspond with annual growth increments.

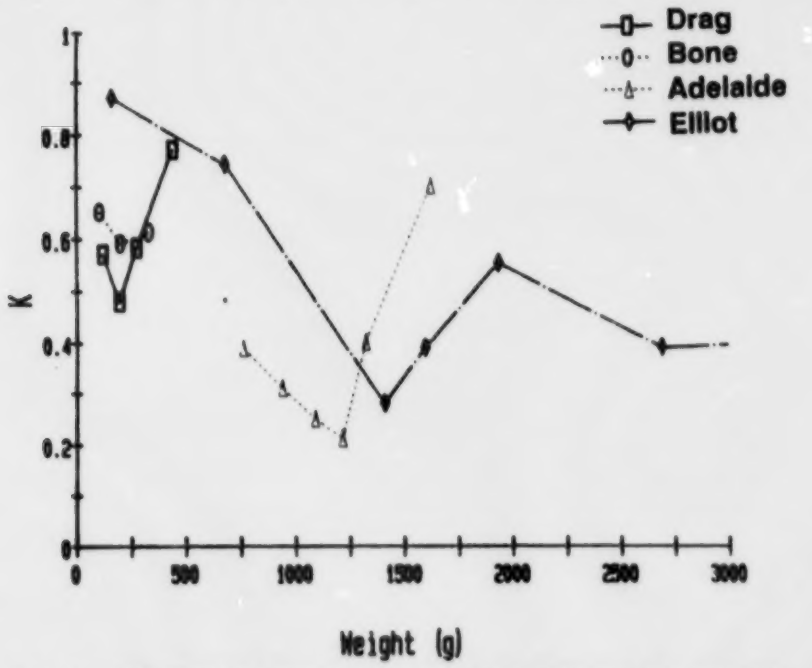


FIG. 7. Relationship between relative growth efficiency (K) and body weight for lake trout from a select set of lakes. Data points correspond with annual growth increments.

lake herring, while two contain round whitefish but no other coregonines. One lake does not contain coregonines.

Of the group of lakes with irregular *K*-lines (Fig. 7), Adelaide Lake and Bone Lake do not contain coregonines, while Elliot Lake has lake whitefish, rainbow smelt, and lake herring. Drag Lake contains lake herring but not lake whitefish.

DISCUSSION

A well documented experiment in growth efficiency occurred in Lake Opeongo in the 1940s (Martin 1970; Martin and Fry 1973). Lake trout in Lake Opeongo exhibited a decrease in growth rate at intermediate sizes. This was attributed to the absence of an appropriately sized food item, even though lake whitefish and round whitefish were present in the lake. Lake herring were stocked in 1944 and 1948, after which lake trout growth efficiency (*K*), instantaneous growth rate (*G*), and age specific production all increased (Carl et al. in press). The analysis of production and instantaneous growth rate described by Carl et al. (in press) corroborated the simple *K*-line approach to examine food web manipulation described by Kerr and Martin (1970) and Kerr and Ryder (1977).

The examination of *K*-lines for different lakes indicated that the **fish communities without coregonines exhibited a tendency to rapidly declining growth efficiency and small maximum size** (Fig. 4). This fits with Martin's (1966) life history model of fish size in relation to percent occurrence of plankton in the diet of lake trout in Algonquin lakes. It is also consistent with the generalization of the life history model by Kerr (1979). Small lake trout feed primarily on invertebrates (zooplankton, benthos), and do not reach a large size because the energetic cost of foraging on invertebrates is high relative to their energy content as the lake trout near a size of approximately 1 kg. Larger trout feed primarily on fish, and are able to grow to a greater size than planktivorous fish because of the efficiency of capturing prey in larger energy units. A small maximum size (1.3 kg) of planktivorous bull trout (*Salvelinus confluentus*) was also observed in a study of an alpine lake population (Carl et al. 1989). This maximum size for bull trout is similar to that revealed by both the planktivorous lake trout *K*-lines and the intermediate size Lake Opeongo lake trout before lake herring introduction, and suggests a common bioenergetic constraint on planktivorous trout.

Some populations, such as Squeers Lake or unexploited lakes in the Arctic, exhibit a bimodal size distribution (Healey 1975; Johnson 1976; Power 1978; Johnson 1983; Ball 1988). These populations are often composed of lake trout which are growing towards an asymptotic size, based on a "planktivore" (invertebrate feeding) *K*-line, or towards an asymptotic size based on a "piscivore" (fish feeding) *K*-line. Kerr (1979) predicted that as soon as a lake trout population with a bi-modal size distribution was exploited, the internal stock structure would disappear. There would not be any "strict" planktivores any more, because the thinning of the population (selective towards larger piscivores) decreased the number of piscivores allowing the planktivorous fish to switch to piscivory (juvenile suppression; Johnson 1983).

The metaphoetesis phenomenon (i.e. shift in feeding behaviour; Hutchinson 1959; Kerr 1979) and our understanding of growth efficiencies makes it possible to describe some community effects in our growth data. Lakes which lack coregonines, or some other suitable prey species, will support lake trout populations which have a small asymptotic size (W_{MAX}) due to bioenergetic constraints of plankton feeding. Such lakes will probably be small in area and have comparatively simple fish communities, following the relation of low species diversity to lake area. Other lakes with suitable prey, such as coregonines, yellow perch, and rainbow smelt, will contain small plankton feeding lake trout that switch to a piscivorous diet when they reach a large enough size. Thus, the growth patterns of individuals within any lake trout population will be composed of one or two stanzas, depending upon fish community composition. It appears that any coregonine, including round whitefish, may suffice to shift the *K*-line to that of a fish feeding population. Growth rate depressions are still possible (e.g. Lake Opeongo before lake herring introduction) for some size ranges of lake trout, due to a lack of proper size prey. However, using *K*-line analyses, these depressions may be identified and the appropriate management action taken. Caution is advised when forming a judgement on a population based on a single year of weight-at-age data, because of year-to-year variation in growth and production (Carl et al. in press). However, **growth patterns represent an extremely valuable ecological clue for diagnosing a production problem** (e.g. Lake Opeongo lake trout, Lac des Mille Lacs walleye - see Colby et al. 1987).

The positive effect that the lake herring introduction had on Lake Opeongo lake trout corrected a growth problem in lake trout in a lake that already had coregonines present. The annual lake trout production (age 8 to 12) in Lake Opeongo before lake herring introduction was only 0.05 kg ha^{-1} (Carl et al. in press). After lake herring were introduced and established a

naturally reproducing population, lake trout production increased to 0.29 kg ha^{-1} (age 8-12). This is similar to the yield from other large unproductive lake trout fisheries and lower than the yield from many small lake trout lakes (Healey 1978).

As suggested in the gillnet ANCOVA, the addition of a coregonine to a benthic/ planktivorous lake trout lake would probably reduce lake trout production, because small planktivorous lake trout would have a lower growth efficiency due to competition with the more efficient coregonines for the same food resources. The larger trout (e.g. those weighing ~1.0 kg) would be able to switch to a piscivorous diet (as shown by a change in *K*) and increase in size because of greater abundance of large-size prey. However, total lake trout production would be expected to drop, since the smaller fish are growing more slowly and the larger fish would be feeding at a higher trophic level with a corresponding loss of energy.

Trophic theory would suggest that production and, hence, potential yield from a "plankton-feeding" population should be greater than that from a "piscivorous" population. Planktivores are cropped at a lower trophic level than piscivores which have increased losses in energy transfer between the highest levels (Kerr and Martin 1970). However, Kerr and Martin (1970) found that observed yields did not vary between these populations as expected. They reasoned that this is a function of the increased energy cost associated with feeding on small particles (plankton). They suggested that yield is simply proportional to primary production and does not vary with the size of the mature fish in the lake. The work of Kerr and Martin (1970) contradicts our finding that yield is higher in small lakes (angling yield of 2.2 no ha^{-1} versus 0.6 no ha^{-1} for lakes less than 256 ha and greater than 2049 ha, respectively; gillnet CUE 2.9 no. 100 m^{-1} versus 1.9 no. 100 m^{-1} for lakes less than 256 ha and greater than 2049 ha, respectively (Table 14)). However, there are several major concerns with their assumption that all lake trout lakes have similar potential yields. First, there is empirical evidence that extremely large standing crops of lake trout may exist in lakes without coregonines. Ball (1988) found that the biomass of fish older than eight years was 7.4 kg ha^{-1} in Squeers Lake (no coregonines). Younger age groups also occurred in the catch and, when these were included, the standing crop of catchable sized lake trout was approximately 21 kg ha^{-1} with an estimate of maximum sustainable yield calculated from a logistic model of 6.7 kg ha^{-1} (P.A. Ryan, OMNR, unpubl. data). The yields from lakes without coregonines in the Sault Ste. Marie area have long exceeded the 0.5 kg ha^{-1} guideline suggested for larger lakes (OMNR 1982, 1983; M.F. Bernier, OMNR, pers. comm.). Second, piscivorous lake trout have passed

through an invertebrate feeding growth stanza and piscivorous populations could sustain higher yield if the fish were taken while still feeding on invertebrates. Third and most importantly, Kerr and Martin (1970) collected yield data for planktivorous lake trout from lakes in Algonquin Park where *Mysis relicta* and other large invertebrates are rarely present (Dadswell 1974). Langeland et al. (in press) showed that lake trout were inefficient planktivores; an inefficiency identified as a high capture cost by Kerr and Martin (1970). Lake trout populations feeding on large invertebrates would presumably support greater yields because of higher energy content per food particle. **We suggest that lake trout feeding on large invertebrates would have intermediate W_{MAX} since bioenergetic constraints would be intermediate to those lake trout feeding on small plankton or fish. Production, and by inference potential yield, would be higher for populations feeding on large invertebrates compared to strictly planktivorous lake trout populations, because of lower costs of capturing prey. Production of lake trout feeding on large invertebrates would also be higher than piscivorous lake trout populations which incur higher trophic level transfer costs.**

Table 14. Lake classification by surface area; illustrating catch and size characteristics of lake trout by lake size classes.

	Lake size class (ha)						
	<128	128-256	257-512	513-1024	1025-2048	2049-4096	>4096
Gillnet Data							
Proportional (%) abundance lake trout (no.)	16.6	17.6	33.8	8.8	13.9	11.6	7.6
Proportional (%) abundance lake trout (kg)	21.7	37.7	42.0	17.9	35.6	26.7	13.8
CUE lake trout (No 100 m^{-1})	2.6	3.3	2.1	1.5	2.2	2.7	1.2
CUE lake trout (kg 100 m^{-1})	6.2	5.0	1.9	2.6	3.5	4.9	1.7
CUE all species (No 100 m^{-1})	25.8	19.0	9.3	55.3	21.0	20.3	20.3
CUE all species (kg 100 m^{-1})	27.2	14.6	9.9	28.4	12.9	18.1	14.6
Lake trout mean weight (kg)	1.11	0.78	1.90	1.90	1.61	2.15	1.72
Angling Data							
HUE (No h^{-1})	0.16	0.28	0.14	0.12	0.15	0.13	0.15
HUE (kg h^{-1})	0.10	0.21	0.11	0.11	0.17	0.16	0.20
Yield (No ha^{-1})	2.7	1.7	1.0	0.9	0.5	0.6	0.7
Yield (kg ha^{-1})	1.4	1.5	1.1	0.9	0.7	0.7	0.6
Mean weight (kg)	0.69	0.75	0.86	1.06	1.3	1.52	1.25
Relative effort (h ha^{-1})	15.4	16.0	17.3	12.7	6.0	6.3	4.31

GENERAL DISCUSSION

The Lake Opeongo growth and production data and the *K*-line results indicate that the **prey species present affect lake trout growth**, while the ANCOVA indicate **predators significantly affect lake trout CUE**. Given these community effects, the FCT concept is relevant and should remain the basis of the FAU program, experimental management, and certain research section efforts until it can be rigorously tested for validity. However, as discussed below, we believe measures of other components of the aquatic community are important and should be examined further for inclusion in a long-term monitoring program.

Several recent papers on lakes Simcoe and Opeongo have confirmed that trend-through-time analysis may delineate community effects on lake trout stocks (Evans and Waring 1987; Shuter et al. 1987; Carl et al. in press). However, the Lake Opeongo work also indicates that the lag time for the effects to be apparent may be up to 10 yr and that normal variation in the system may further confound detection of real change. The empirical evidence from Lake Opeongo suggests that trend-through-time data should be collected for a minimum of 10 to 20 yr, with little or no interruption in the annual collection to be effective in detecting changes in lake trout systems. This is similar to the time of one generation of the oldest species in the system recommended by Christie et al. (1987) to monitor aquatic systems for change, and again indicates the requirement for long-term, continuous monitoring of aquatic systems.

The Lake Opeongo and Simcoe examples both involved long-term data collection during which non-indigenous fish were introduced (e.g. lake herring in Lake Opeongo and rainbow smelt in Lake Simcoe). Thus, changes were detected through comparison with pre-introduction data. In order to determine the effects of community interactions or changes in a variety of systems in which no pre-disturbance data are available, it is necessary to collect trend-through-time data on such lakes and make broad comparisons. In other words, intensive serial data over a variety of lakes (spatial data) will be required to understand mechanisms causing the effects noted in the ANCOVA and growth analyses. This enumeration of community effects was a principal reason for establishing the FAU program, and remains very important for now and in the future. The continued collection of lake trout population data, on an annual basis, and key fish species data 2 years in 5 (until we determine more precisely how often it should be collected; e.g. set the test power at the appropriate level, Peterman 1990) by the FAU program is necessary. The support by research and

management personnel in analyzing and transferring this knowledge will allow development of management systems for protecting the lake trout resources of the province from man-induced perturbations. As indicated above, **fisheries managers should be aware that 10-20 years of annual collection of serial and spatial data will be necessary before many underlying mechanisms are understood** (one generation; Christie et al. 1987). The alternative is to continue to manage with a poor knowledge base and face serious criticism for our lack of science in management.

A considerable amount of energy has been expended by the OMNR in developing the community approach to fisheries assessment and management. The analyses in the present report were limited to the available fisheries data, and seriously restricted the discussion of trophic level effects. As part of a community approach, key features of aquatic communities besides fish should be identified that may separate out lakes which respond to perturbations in a similar manner or indicate when a lake trout population is being overharvested. Recent work has indicated promising new areas to investigate that may lead to greater understanding of lake trout communities. A short list of these community based "key features" should be considered for addition to the FAU and lake survey data collection lists. These features may, in part, describe the food web that is supporting aquatic production in a given lake and, ultimately, may improve our ability to manage lake trout lakes. We therefore examine several key features in the following discussion.

Habitat characteristics, such as surface area, water depth and chemistry establish the general ecological relationships in a lake among the fish, zooplankton and phytoplankton. The predatory behaviours and efficiencies of the fish species and invertebrate predators drive the system, as predicted, from the model of size dependent and gape limited predation developed by Zaret (1978, 1980) and quantified by Mills and Schiavone (1982). The latter authors observed the relationship between the average size of fish and zooplankton across a group of lakes. Lakes with substantial game fish populations usually had zooplankton communities dominated by large species. Where the average size of the zooplankton was small, the lake contained large numbers of small plankton feeding fish species, and few game fish. This empirical relationship was developed using very simple practical indices. Collection of zooplankton for size measurements were made by standard plankton nets and protocols (Mills and Schiavone 1982). A second zooplankton index of daphnia size has been formulated that shows promise in distinguishing levels of predation on large herbivorous zooplankton in oligotrophic systems (Langeland et al. in press).

Interestingly, Mills and Schiavone (1982) found the relationship between fish and zooplankton

was not clear when the large invertebrate predator *Mysis relicta* was present. The importance of *Mysis relicta* in the structuring of aquatic communities has been indicated by changes in the zooplankton and fish communities following its introduction into new waters (Rieman and Bowler 1980; Lasenby et al. 1986; Langeland 1987). The immediate impact usually involves the loss of any large herbivorous cladocerans (e.g. *Daphnia* sp.) with subsequent decline in growth rates for the species that feed on them. In Pend Oreille Lake, Idaho, a piscivorous lake trout population fed on kokanee salmon (*Oncorhynchus nerka*) which in turn fed on zooplankton. After *Mysis* was introduced in the lake, the kokanee population collapsed and never recovered. The decline of the kokanee population was presumed to be due to competition with *Mysis*, in large part for herbivorous cladocerans, that led to poor growth and small size of kokanee. This was followed by predation by lake trout. Currently the lake supports a small-sized lake trout population feeding on *Mysis*. Structural changes in the zooplankton community appear to be long lasting, since the absence of large cladocerans also occurs where *Mysis* is endemic (Langeland et al. in press).

We speculate from this kokanee example, and discussion by Colby et al. (1987), that *Mysis* is able to reduce the number of large cladoceran zooplankton to a level that less efficient planktivores such as the coregonines would show poor growth rates and, that in inland lakes, *Mysis* are often not suppressed by fish predation. This poor planktivorous fish growth in lakes with *Mysis* introduced, coupled with predation on the coregonines by lake trout, may lead to a long-term suppression of the coregonine population, in a manner similar to the kokanee example. With a reduced coregonine population, the lake trout population would also shift towards a predominantly benthivorous-planktivorous *K*-line and feed on *Mysis* directly. Lake trout production might increase as lake trout feed at a lower trophic level, as in Squeers Lake where *Mysis* are present. The mean size of lake trout should decline as they switched from fish to smaller-sized prey. However, in White Partridge Lake, Ontario, lake trout size and yield are small and the shortjaw cisco (*Coregonus zenithicus*) and *Mysis* are present. This suggests that the effect of *Mysis* may be quite complex and require further investigation.

Given the evidence in the literature and the examples of Pend Oreille Lake and White Partridge Lake, **the presence/absence of *Mysis* may be a key descriptive or classifying feature of lake trout lakes**. It is a native species which is widely distributed in Ontario lakes (Dadswell 1974; Black 1983), with the exception of some higher altitude lakes such as those in Algonquin Park (Martin and Chapman 1965). **Part of the unexplained variance in lake trout production in lakes**

with planktivorous fish may be due to trophic level effects, depending in part on the presence or absence of *Mysis*.

Christie et al. (1987) used a sine wave model to describe the behaviour of pelagic food webs. In this model, adjacent levels are negatively related and alternating trophic levels are positively related. For example, if large predators are abundant then planktivorous fish are reduced in numbers due to predation. Large zooplankton are abundant because of reduced predation by planktivorous fish, while the phytoplankton populations are reduced in size because of predation by the abundant zooplankton. This model is an interesting framework for examining lakes without regard to species, and provides a theoretical framework for the relationship between fish and zooplankton developed by Mills and Schiavone (1982). **The sine wave model may be a powerful analytical tool and offer a different perspective for examining community dynamics.**

A gillnet data set (T.R. Marshall and P.A. Ryan, unpubl. data) provided an example of how the sine wave model may be applied to lakes. In this example, we make no attempt to examine size distribution of plankton. Only small and large fish presumed to be planktivorous and piscivorous, respectively, are examined. The fish weight data were $\log_2$ transformed and plotted versus the percentage composition of the catch. A family of biomass distribution curves was plotted based on the composition of the survey catch (by weight; Fig. 8). Fish communities that anglers value usually have high numbers of large species (*K*-selected species, Fig. 8d and 8e). The opposite extreme is illustrated in Fig. 8a, representing lakes with the greatest abundance of small species (*r*-selected species), usually due to overharvest of large fish. Intermediate states are illustrated in Fig. 8b and 8c. Once standard curves have been established, a fisheries manager might determine where a given lake was in the range of this community characteristic, by comparing the size composition from a representative gillnet survey of the lake to a range of size distributions, such as that illustrated in Fig. 8.

We presume communities which have a low concentration or abundance of small species are stable over time, because a high degree of internal regulation is provided by large piscivores which control planktivorous fish (Christie et al. 1987). Such a community probably supports, or can support, a high quality fishery. Excessive fishing or other stresses may lead to a departure from such a condition and a degradation of fishing quality, due to increased abundance of small planktivorous fish.

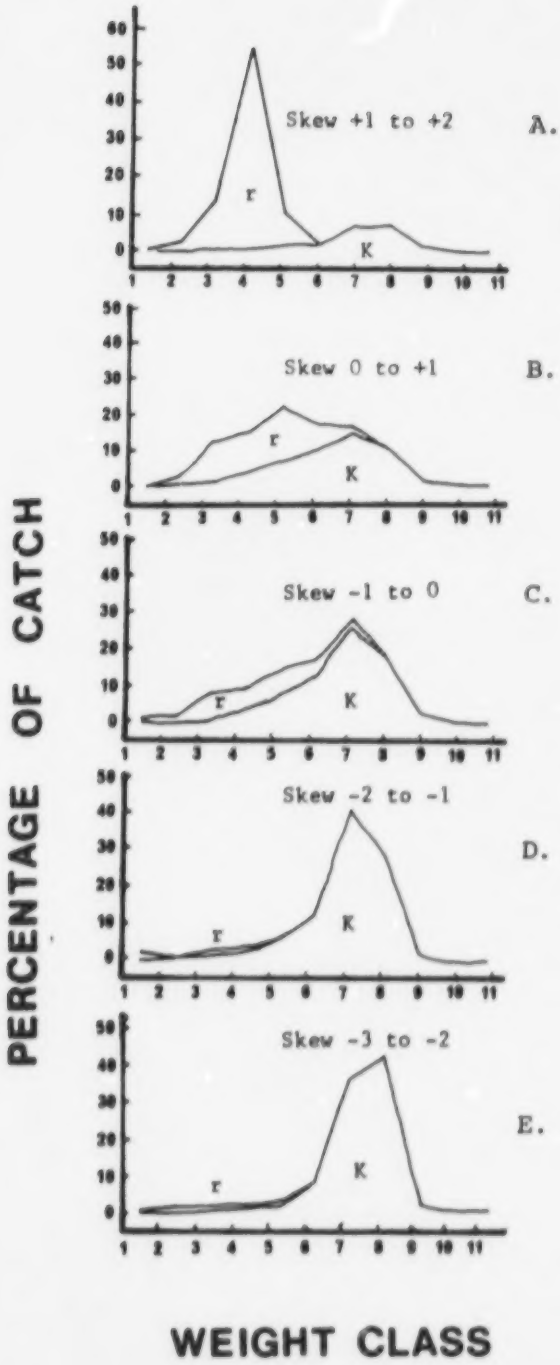


FIG. 8. Size distribution of fish in $\log_2$ weight classes (g) taken by gill net.

This collection of size distributions was assembled in order to describe the "range" of this characteristic as a first step to lake classification without regard to fish species. **Expansion of the family of biomass curves, to include many lake trout lakes from across the province, would provide a manager with a standard against which to compare the fish community in a particular lake.** We caution that valuable fish communities, such as those supporting "planktivorous" trout populations, may not necessarily fit the extreme "large fish dominant" distributions.

While this approach offers some opportunity to fingerprint community states from the fish perspective, without a great deal of further development, it may be possible to distill the information down to an index of fish particle size. This fish size index could be used with other measures, such as mean size of zooplankton (Mills and Schiavone 1982), the Daphnia Size Index (Langeland et al. in press), or direct measurement of zooplankton size composition (Sprules 1984). **Together, these measures would be useful for diagnosis of the health of the food web and fish community in a lake, if incorporated into a simple community model.** It may be found through additional research that only one or two of these indices are needed to identify where, on a clinal basis, a fish community is, in terms of community dynamics. Thus, these indices hold some promise of reducing the data needed to manage lakes.

In summary, it was implicit in the original fish community approach, based on the presence/absence of six species, that we were attempting to categorize lakes together that respond to changes in a similar manner. **Perhaps some of the large variation in lake trout parameters we noted within FCTs would be explained by further categorizing lake communities by the presence or absence of coregonines and large invertebrates. These key factors indicate the type of food web present in a lake and what the potential yield may be.** The zooplankton index and fish particle size analysis show the current state of a lake (i.e. exploitation level). The two types of information provide us with the means to improve our prediction of lake trout yield and should be developed further and monitored in the FAU program. The FCT model, and incorporation of the non-fish indices discussed above, are an excellent start at understanding community interactions in lake trout lakes. With the addition of serial and spatial data from the FAU program, a strong predictive community model is quite feasible.

A different approach which may be useful is to manage lake trout lakes on the basis of lake area. Lake area was found to be highly correlated with each of the measures of community structure, many of the measures of lake trout catch and harvest, and most of the other abiotic

variables included in the analyses. It would appear that there are several community and abiotic variables which change with lake area and, therefore, cannot be readily separated with the comparative creel data sets available to us. The catch, relative abundance and growth characteristics of lake trout from lakes classified by surface area would reflect the sum of the biotic and abiotic effects that lake size integrates. From a management perspective, a simple classification system using area categories is desirable, because of the general inferences on lake trout yield that appear to be possible, based on area alone. **An important shortcoming of an area model which managers should keep in mind is its difficulty in giving a detailed picture of the population and in predicting shifts in the dynamic state of the aquatic community. The impact of fish introductions or other perturbations may be better anticipated by using knowledge of the community in question along with community theory** (Evans et al. 1990).

A classification system was examined based on a $\log_2$ scaling of surface area. This resulted in seven classes by area within which lake trout lakes of Ontario are fairly evenly distributed (Table 15). When fish community characteristics for lakes in these size-classes are compared (Table 15), a major shift in community structure appears evident for lakes in the 257-1024 ha range. Many fish species first appear in lakes in the 257-1024 ha range, most notably lake whitefish and lake herring. Lakes in the smallest size-classes exhibit simple fish communities with, at most, two major species present and no more than one predator occurring, in addition to lake trout. Those in larger size-classes are characterized by complex communities, composed of three or more major species.

The simple community classification separates lakes differing in some, but not all, catch characteristics (Table 14). There may be a pattern among the two smallest lake area size-classes and the two largest in the proportional abundance and CUE of lake trout. Both measures are slightly larger in the small lakes. The CUE of all species combined from gillnet catches, and HUE of angled trout show no apparent trend. However, there are trends across the lake area classes in the mean weight of lake trout and the other angling harvest variables, and the presence/absence of major species. Similarly, lake trout mean size becomes progressively greater as lake size increases in the gillnet data set. As with the community attributes, a major shift occurs across the 256-1024 ha size-class.

We suggest a simple community classification system based on lake surface area may help managers determine a rough boundary on what a given lake may produce (Table 16). A transition among lakes occurs across a size range of 257 to 1024 ha, with the fish community and catch

characteristics of lakes differing greatly between smaller (<256 ha) and larger (>1025 ha) lakes (Table 14 and 15). Within each of these two groups, however, the variance appears to be fairly low. It is thus possible to condense these seven area categories classes into three (Table 16). **It should be remembered that suggested yields are general in nature only and are for lakes in which the lake trout population is not overexploited, and relies on natural reproduction rather than hatchery stocking.**

Small lake trout lakes (<256 ha) are relatively deep, with low diversity of species, no coregonines, and no more than one predator in addition to lake trout. These lakes may support high densities of small, planktivorous/benthivorous lake trout, and relatively high angling yields (frequently 2.0 kg ha^{-1} or more).

Large lakes (>1025 ha) have many fish species present. Coregonines are present, along with a number of other major species which may be competitors with lake trout. Lake trout use coregonines as forage, reach a large mean size, have low standing stocks, and provide a smaller yield to anglers (frequently less than 0.5 kg ha^{-1}).

In intermediate-size lakes (257-1024 ha), if the fish community composition resembles that of small lakes, the sustainable yield for lake trout may also be expected to be similar. On the other hand, if a complex community occurs (with suitable fish prey), lake trout would have the same attributes, including yield, as in the large lakes.

To provide perspective, examples are given in Table 17. Dickey, Pringle and Bone are typical small lakes and support high angling yields. Lake of Bays, Opeongo, Temagami, and Aylen are large lakes and have low yields of lake trout. One of the medium-sized lakes (White Partridge), has a complex community, and provides a low yield, while three others (Flack, Squeers and Scattergood), have simple communities and support a high yield of lake trout. Megisan and Anstruther are intermediate in both community complexity and yield.

The validity of using lake area in a community classification scheme might be questioned, given the weak relationship between lake trout gillnet CUE and lake area. However, the gillnet correlation analysis indicated that the presence/absence of all predators and coregonines were strongly correlated with lake area. The lake area classification system, therefore, holds some promise as a general guideline for lake trout yield, but it must be further investigated to determine its usefulness to managers. **A good start at understanding an individual lake would be to collect the requisite biological data and categorize the lakes as outlined in Table 16. This would give**

Table 15. Lake classification by surface area, illustrating community attributes by size class. A '+' indicates the species occur in much more than 50% of lakes within the size class, a '0' indicates occurrence in much less than 50% of lakes, and a '0/+ indicates occurrence in approximately 50% of lakes.

	Lake size class (ha)						
	<128	128-256	257-512	513-1024	1025-2048	2049-4096	>4096
Species diversity (wt)	1.62	1.18	1.47	2.14	1.89	2.13	2.25
(No)	1.35	1.38	1.69	2.17	2.17	2.12	2.38
# major species	1-2	2	2-3	2-3	3	3-4	4+
# additional predators	0-1	1	1-2	1-2	1-2	1-3	2-3+
Community complexity	Simple	Simple	Simple/complex	Complex	Complex	Complex	Complex
Community Attributes							
Walleye	0	0	0	0	0	0/+	+
Burbot	0	0	0	0/+	0/+	+	+
Northern pike	0	0	0/+	0/+	0/+	+	+
Brook trout	0	0	0	0	0	0	0/+
Smallmouth bass	0	0	0	0	0	0	0/+
Walleye/northern pike	0	0	0/+	0/+	+	+	+
Walleye/burbot	0	0	0/+	+	+	+	+
Yellow perch	0	+	+	+	+	+	+
Rainbow smelt	0	0	0	0	0	0	0/+
Lake herring	0	0	0/+	+	+	+	+
Lake whitefish	0	0	0	+	+	+	+
Coregonines	0	0	+	+	+	+	+
Coregonines/smelt	0	0	0/+	+	+	+	+

Table 16. General characteristics of naturally reproducing lake trout lakes in relation to lake size.

Abiotic characteristics	Community characteristics						Lake trout characteristics		
Lake size (ha)	No. of major species	No. of additional predators	Community complexity	Coregonines present	Prey size	Mean size	Biomass (kg ha^{-1})	Gillnet CUE (kg 100 m^{-1})	Angling yield (kg ha^{-1})
Small <256	1-2	0-1	Simple	No	Plankton Benthos	Small	High	High	High
Medium 257-1024	2-3	1-2	Variable	Variable	Mixed	Variable	Variable	Variable	Variable
Large >1024	4-6	1-3+	Complex	Yes	Fish	Large	Low	Low	Low

Table 17. General relationship between lake trout sustained yield (e.g. lakes have sustained moderate effort for a number of years and contain healthy lake trout populations) and lake size. The following species present in each lake are enclosed in brackets and coded as follows: BT = brook trout, Wa = walleye, NP = northern pike, SB = smallmouth bass, RS = rainbow smelt, LW = lake whitefish, LH = lake herring, Bu = burbot.

Lake size (ha)	Lake trout potential yield (kg ha^{-1})						
	0-0.4	0.4-0.8	0.8-1.2	1.2-1.6	1.6-2.0	2.0-2.4	>2.4
Small <256					Big Clear 187 ha (SB)	Pringle 182 ha (none)	Big Salmon 148 ha (SB)
					Dickey 214 ha (SB)	Bone 122 ha (none)	
Medium 256-1024	White Partridge 575 ha (BT,Bu,LH)	Drag 1004 ha (SB,LH)	Louisa 490 ha (none)	Flack 951 ha (Bu)		Squeers 384 ha (NP)	
		Megisan 628 ha (RS)	Anstruther 634 ha (SB)			Scattergood 282 ha (none)	
Large >1024	Aylen 2016 ha (SB,LW,Bu)	Opeongo 5860 ha (SB,LW,LH,Bu)					
	Lake of Bays 6904 ha (SB,LW,LH, Bu,BT,RS)	Temagami 20972 ha (SB,LW,LH, Bu,NP,Wa)					

the manager a sense of what the lake should be producing. We would like to stress that this simple model needs further development to determine its usefulness in communities without lake trout. The system would be of greater practical use if it showed similar benefits for percid or other communities.

CONCLUSIONS

We could not detect statistical differences in lake trout abundance and yield among lakes classified on the basis of FCT, however, the tests we used were relatively weak because of small sample size and autocorrelation among independent variables. The angler harvest of lake trout is related most strongly to angling effort, and secondarily to lake size; angling data do not allow a valid test of community effects because of this correlation. The relative abundance of lake trout (measured by gillnet CUE) is strongly related (negatively) to the numbers of fish predators occurring in the lake. Burbot and northern pike appear to be the most important species in this regard. The presence of coregonines is also negatively correlated with gillnet CUE. Growth patterns of lake trout may be a valuable diagnostic tool for measuring problems in lake trout communities. Higher standing stocks of lake trout tend to occur in smaller lakes. This is likely due to lower trophic level transfer costs as most lake trout populations in these lakes are benthivorous/planktivorous in nature with small maximum size and with growth efficiency rapidly declining with increasing size. Lakes with benthivorous/planktivorous lake trout will provide more fish as weight harvested but of smaller size to a fishery.

MANAGEMENT RECOMMENDATIONS

Inland lake trout lakes should be considered in two groups for management purposes (a) with and (b) without coregonines or other suitable prey. Lakes with coregonines will provide larger fish to a fishery, due to a bioenergetic advantage over planktivorous/benthivorous lake trout populations, but have a lower sustainable yield. Annual collection of lake trout population data on monitored systems, whether FAU or district, is essential to separate out stochastic variation from perturbation effects. Data on other parts of the aquatic community should continue to be collected 2 in 5 years until we can determine more precisely how often it should be collected.

The FCT concept should continue as the basis for the FAU program. We should examine non-fish components of the communities for incorporation into the FCT approach. Indices (the presence/absence of *Mysis*; zooplankton size structure; overall fish size frequency distribution; lake trout growth patterns) which define community state may contribute to an improved lake trout model and should be examined further.

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